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THE

AMERICAN NATURALIST

A CONTRIBUTION TO THE LIFE HISTORY OF AUTODAX LUGUBRIS HALLOW., A CALIFORNIAN SALAMANDER.

WM. E. RITTER AND LOYE MILLER.

Autodax is a genus of salamanders confined, according to our present knowledge, to western North America and almost entirely to California. Three species are known, namely, *A. lugubris* Hallow., *A. ferreus* Cope, and *A. iëcanus* Cope. The genus belongs to the Plethodontidæ and is undoubtedly close of kin to Plethodon itself. *A. lugubris*, the most common and best known of the species, is, however, according to Cope ('89), "one of the most marked species of North American salamanders," and it is an interesting and suggestive fact that all the zoölogists who have written concerning members of the genus have noted about them various reptilian characteristics either of structure or habit. Thus, Spencer Baird ('52), one of the earliest observers of *A. lugubris*, the subject of the present paper, mentions the unusual size of the teeth and compares the undulating outline of the mouth to the mouth of the alligator; and Charles Girard ('58) makes the same comparison. Cope ('89) points out these reptilian assimilations in the following words, his remarks having reference to *Autodax lugubris:* "This is one of the most marked species of North American salamanders. The large temporal muscles give the head a swollen outline behind and separate the derma from the cranium. The latter adheres to the top of the prominent muzzle. The fissure of the mouth is sinuate, most strongly so in adult specimens. On the whole, the physiognomy is not unlike that of the snapping tortoise. I have little doubt that it is more capable of inflicting a bite than any other of the American Urodela."

Dr. John Van Denburgh ('95), who has had much more opportunity than any of the preceding writers to observe Autodax alive, makes these statements about the habits of *A. iëcanus:* "It usually walks quite slowly, moving but one foot at a time, but it is capable of motion surprisingly rapid for a salamander. When moving rapidly, it aids the action of its legs by a sinuous movement of its whole body and tail.

"The tail of this Autodax is prehensile. Several individuals, when held with their heads down, coiled their tails around my finger, and, when the original hold was released, sustained themselves for some time by this means alone. One even raised itself high enough to secure a foothold. This animal's tail is also of use to it in another way. When caught, *Autodax iëcanus* will often remain motionless, but if touched will either run a short distance with great speed, or, quickly raising its tail and striking it forcibly against the surface on which it rests, and accompanying this with a quick motion of its hind limbs, will jump from four to six inches, rising as high as two or three."

Most of these observations by Van Denburgh we have many times confirmed in our experience with *A. lugubris,* although we have never seen it jump on a level, nor to so great a distance as that mentioned by this writer. When wishing to pass from an elevated position to a lower level, as, for example, from the hand to the table when the former is held some inches above the latter, instead of falling over the edge in the typical salamander fashion, the creature will frequently execute a well-coördinated spring and alight on its feet some distance away.

The quickness of movement of Autodax, as contrasted with the general sluggishness of the typical salamander, is striking indeed.

Although the illustrations given by Cope ('89), p. 184, show fairly well the characteristics of the head mentioned by him, in several respects these are really more marked in fully grown specimens than his figures indicate. We have, consequently, thought it best to supplement his illustrations. Figs. 1 and 2 are dorsal and lateral views of the head of a large male.

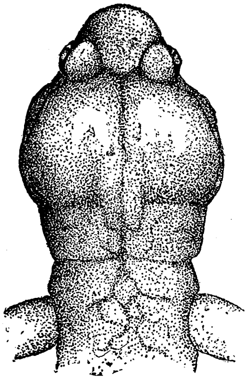

Fig. 1.

The teeth of the projecting upper jaw in adults are distinctly visible when the mouth is closed, their points not being covered by the lip (Fig. 2). Further, their large size causes ridges on the outer surface of the lip. Professor Cope's conjecture that the animal is capable of inflicting a bite is certainly very reasonable, but we have been unable to get any positive evidence on the point.

The species is entirely terrestrial and seems to be indifferent even to a proximity to water. Rotten stumps and logs are the preferred habitations, and wherever these occur in the region about San Francisco Bay, even though at the remotest places from water, specimens are almost sure to be found, and frequently in considerable numbers in or under the same stump. Thus a single stump at Sausalito, Marin County, yielded to one of us seven specimens of one size and five of another size, none of them, however, being fully grown. Those of the smaller size were about 50 mm. long, and were dark gray, almost black, in ground color, with finely sprinkled bluish silver. Those of the large size were about 75 mm. long, were much lighter in ground color, and were wholly devoid of the silvery specking, but possessed a few relatively large yellow spots

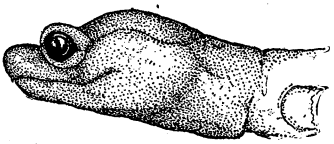

Fig. 2.

on the sides of the abdomen. As we now know, the smaller darker ones were of last year's hatching; and in all probability the larger ones were a year older. The presence together of so many individuals suggests that those of the same size all belonged to the same brood; and also the possibility that the two broods represented were both the offspring of the same parent. Of course there was no way of answering this query positively, but one other piece of information that we have obtained confirms the suggestion in so far as it furnishes farther evidence that the young of a brood may remain together for a considerable period after hatching. Some time during March, 1896, a student in zoölogy, whose testimony we regard as reliable, reported to one of us that he had found a fully grown salamander, which, from his description, was undoubtedly Autodax, "with a lot of little ones."

The species is decidedly nocturnal in its habits. This is not only proven by the fact that one practically never finds it abroad during the daytime in nature; but also by the alacrity with which specimens kept in confinement in a terrarium seek to secrete themselves during the daytime, but come out and run about freely during the night.

As shown by Wilder, Autodax is, in common with so many of the long-tailed amphibians, lungless. This being so, the exclusively terrestrial habit of the animal makes the question of the seat of respiration in this species particularly interesting.

We do not propose to go at length into a discussion of this subject at present, but content ourselves with noting a few observations that support the view recently defended with special emphasis from the morphological side by Bethge ('**98**), that, in the absence of both gills and lungs, respiration is performed by the mouth epithelium and the integument together, each taking an essential part. This is in opposition to the conclusion drawn by Camarano ('**94**), in particular, from physiological studies on *Salamandrina perspicillata* and *Spelerpes fuscus*, both lungless salamanders. This author believes that the skin participates very little, if at all, in respiration.

The facts which we interpret as meaning that the integument takes an important part in respiration are these: In the first place, the softness, delicacy, and constantly moist condition of the skin of the entire body, and the abundant supply of blood vessels and capillaries within it, furnish the structural conditions necessary for respiration. In this connection the vascular supply to the toes deserves particular attention.

A great blood sinus is present on each side, and near the end of each of these organs (Fig. 3).

These lakes of blood, as they may be called, become particularly conspicuous in animals that have been anæsthetized with ether or chloroform, though they are easily seen by the aid of a hand lens in the normal living specimens. It is a reasonable supposition that we have here a not unimportant seat of respiration. No portion of the integument is better calculated to make the most of what little moisture there may be in the animal's surroundings, they being especially adapted to this end both as regards contact with moist bodies and area of surface exposed. The toes, in fact, may be considered to have assumed in a measure the function of external gills.

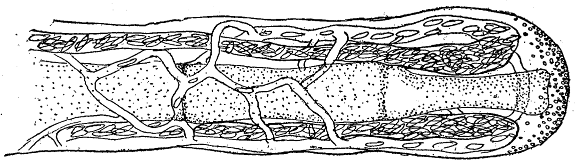

Fig. 3.

How generally this vascular condition of the toes is among the amphibia we do not know. In two other species having much the same habits, at least as regards dwelling places, which we have examined, namely: *Plethodon oregonensis* and *Batrachoseps attenuatus*, practically the same conditions are found, while in *Diemyctylus torosus*, the habits of which are quite different, and in which lungs are present, no unusual degree of vascularity is found in the members.

The toe-tips of Autodax are somewhat expanded (Fig. 3), and the animal has considerable power of clinging by means of them to vertical and overhanging surfaces. In this respect it resembles Hyla somewhat, and consequently a comparison between the two forms with respect to toe structure is suggested.

Examination of the toes of living specimens of Hyla reveals the fact that here also the tips — pads, as they are well known to be in this animal — are rather richer in capillaries than are other portions of the feet and limbs, but the blood sinuses are not present. Schuberg (**'91**) has made a detailed study of the toes of the *Hyla arborea*, and although he does not particularly discuss the blood supply to the organs, his figures show not only that the sinuses are absent here, but they seem to indicate that blood vessels and capillaries are not especially abundant.

That the pharynx also plays an important part in respiration is indicated by the constant vibration of the region. From 120 to 180, or even more, of these vibrations take place in a minute, and in some cases they are grouped into series of about twenty to twenty-five extremely rapid vibrations, with periods between each two series during which the vibrations almost entirely cease.

The supposition that these vibrations are respiratory is strengthened by the fact that when the animal is immersed in water they cease entirely, the floor of the mouth and pharynx being then held permanently compressed against the upper wall, apparently for the purpose of excluding the water. In this respect Autodax differs markedly from Diemyctylus, where the pharyngeal floor may or may not vibrate while the animal is out of the water, but always has a constant, though much slower, up-and-down movement during aquatic periods of life, Gage (**'91**), Ritter (**'97**).

For the little published information we have regarding the reproduction of Autodax we are indebted to Dr. Van Denburgh. On July 25, 1895, this herpetologist received from Los Gatos, Cal., a female specimen of *A. iëcanus* with fifteen eggs. A note accompanying them stated that they were found "under the platform in front of a barn, in dry earth next the foundation wall, and about fifteen inches or more below the surface. . . . There was no water within ten or fifteen feet." Dr. Van Denburgh did not hesitate to consider the eggs to belong to the Autodax, as he found entirely similar ones in the ovaries of another specimen taken from the same locality on July 30 of the same year. The female accompanying the eggs had numerous small ovarian ova. The eggs, the author says, were in the early stages of segmentation. Unfortunately, this is all the information he gives us concerning them, and he tells me now that he tried to keep them alive in order to watch their development, but that in this he was not successful.

The specimens upon which our observations have been made were found on the grounds of the University of California by one of the students. They consisted of an adult female and nineteen embryos, all in practically the same stage of development and well advanced. They were found slightly beneath the surface of the ground and close under the oversetting base of a large palm tree.

The student who found them stated that he noticed, as he was loosening the earth about the roots of the palm, a hole which he at first supposed to be a gopher hole, but on removing a little of the soil at this point the salamander and her eggs were brought to light. He says that on being uncovered and disturbed she "squeaked like a mouse." This sound was one of the first things that attracted his attention. This squeak is frequently produced by adults when first taken, but rarely while they are in confinement. They were on the south side of the tree; and as the ground in this palm grove is kept perfectly free from other vegetation, and the spot where the animals were located receives the full force of the sun's heat during the whole middle portion of the day, it will be readily understood, particularly when it is considered that this region had received no rain for at least two months, that the place was about as dry as it can become. There is a creek bed about fifty meters from the tree, but this had been dry for three months at least.

When brought to the laboratory in a box with some earth, the salamander was partly coiled around the eggs, and in this position she seemed at first inclined to remain, since she returned to the eggs several times after being removed. The following morning, however, she had left them and appeared to have entirely deserted her charge. As we had arranged her new habitation in such fashion as to make the conditions as nearly natural as possible, we concluded that it was useless to expect the parent to care any longer for her family, so determined to take charge of them ourselves, and to make use of her to settle by dissection various anatomical and physiological questions that had arisen.

From the evidence at hand, then, there can be no doubt that Autodax lays its eggs not only in the earth, but in earth that may be very dry; that at least most of the development of the embryo takes place after the eggs are laid; and that the female parent remains with her eggs most of the time during the development of the embryo.

For what purpose the female tends her eggs is not entirely clear, but it is almost certain that one end attained is the maintenance in them of the high degree of moisture essential to their development. We supposed, on receiving the embryos and learning of the place where they had been found, that it would be necessary, in order to insure their further development, to place them under conditions of temperature and dryness similar to those by which they had been surrounded in nature. We consequently prepared a terrarium with this end in view, but greatly to our surprise and consternation, on the following morning we found the eggs much shriveled and most of the embryos either dead or nearly so; and it was only by placing them in water and allowing them to remain there for an hour or more that we succeeded in restoring any of them to their former healthy, active state. Four embryos returned to full vigor; and by keeping these on damp earth, and thoroughly wetting them at least twice a day, they continued to develop apparently in a perfectly normal way, to the time of hatching, which was September 13, or about fifty days after they were taken.

How do the eggs in nature get the large amount of moisture necessary to their life and development? Through a long series of observations made under the direction of Professor E. W. Hilgard of the Agricultural Department of the University of California, during the past extremely dry season, it has been proven that plants draw moisture from the soil after a degree of dryness has been reached, which has generally been believed to be incapable of yielding any moisture to vegetation; *i.e.*, after microscopic water is no longer present. It may be that this fact is not without significance for such animals as our land-dwelling salamanders also. But we can hardly believe that such moisture can do more than prevent evaporation to some extent. It does not appear to us possible that sufficient water to insure the development of the eggs can be derived from this source. Our specimens were always more or less completely covered, and as the earth on which they were kept was constantly wet almost to saturation, and as they were not subjected to the direct heat of the sun at any time during their confinement, the evaporation from them under the artificial conditions could hardly have been greater than that under the natural conditions; and it appears impossible that any such quantity of water could be drawn from the dry soil in which they were found as it was necessary to give them each day to prevent desiccation.

The possibility that the urine of the parent might be the chief source of moisture to the embryos was suggested by the large size of the urinary bladder, and it is by no means impossible that the suggestion is well founded. However, a study of the structure of the organ and a comparison of it with its counterpart in other species where it is certainly not put to such a service do not confirm the conjecture. The bladder of Autodax does not differ either in size or minute structure from that of Diemyctylus, for example, the young of which are hatched in water. In fact, the bladder of Diemyctylus is of the two-lobed type, while that of Autodax is not lobed, and hence may be looked upon as the simpler of the two.

(See Field ('94), for a discussion of the different types of amphibian urinary bladder.)

The Embryos and their Development.

As already said, there were nineteen embryos in our batch. Each was contained in a gelatinous capsule and was firmly anchored to a clump of earth by a narrow peduncle, about 8 mm. long, composed of the same material as the capsule. The peduncles were attached to the earth close together; in fact, their adhesive, expanded, attached ends were more or less confluent (Fig. 4).

The peduncles were twisted, and each appeared to be hollow. The capsules were rather thin and seemed decidedly leathery when the eggs first reached us — as was always afterwards the case if the eggs were permitted to desiccate to any extent. After having imbibed water, however, which they did very eagerly, they became much thicker and more transparent and showed clearly their gelatinous nature.

The capsules were almost perfect spheres, and in what might be considered their normal state as regards imbibed water, were about 6 mm. in diameter. When the capsules were moderately swollen, and their surfaces were washed clean, the black embryos and the very large yellow yolk-sacs could be distinctly seen through them; and many details of structure were studied from day to day on the living specimens as they continued to develop. Figs. 5 and 6 were drawn from living specimens.

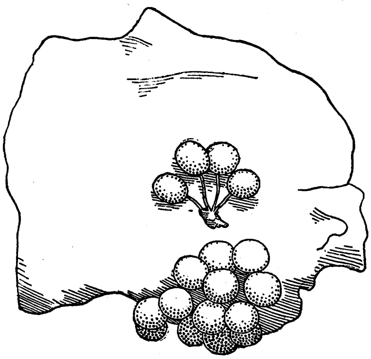

FIG. 4.

Four days after they came into our possession one embryo was dissected from its capsule and was found to be 15.5 mm. long. Its fore and hind limbs were of nearly equal length and were about 2 mm. long. The toes had not yet appeared. The gills were very large, and were each composed of three broad membranous lobes (Figs. 5 and 6).

The facts of special interest concerning the embryos, and which, consequently, we consider somewhat more in detail, are the following:

(1) *The Great Quantity of Yolk in the Eggs, and the Vitelline Circulation.* — The yolk-sac of the embryo, measurements of which are given above, was 5 mm. in diameter. This is a little more than twice the diameter, or eight times the mass of the eggs of *Diemyctylus torosus*, a species of about the same size as *Autodax lugubris*, but one in which the eggs have about the character, as regards yolk, of amphibian eggs in general. Whether or not the egg is meroblastic we have been

unable to determine with certainty, though what evidence we have obtained points to the conclusion that they are of this type. We have been unable to find any trace of either nuclei or other protoplasmic material, or cell boundaries, in the sections of the yolk which we have made. But, of course, earlier stages of development will have to be studied before the point can be definitely settled.

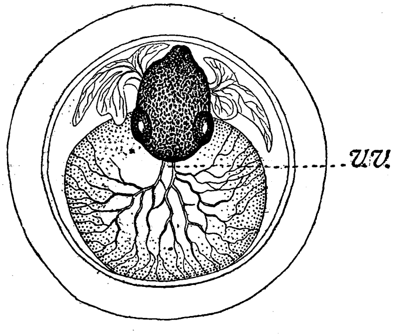

FIG. 5.

The entire surface of the yolk is covered by a very delicate epithelium which carries the vitelline vessels and capillaries. No pigment is present excepting in the embryo itself.

The general character of the vitelline vessels is shown in Figs. 5 and 6. The vitelline arteries, *v.a.*, are given off from the dorsal aorta in pairs, there being approximately a pair for each myotome of the abdominal region of the embryo. In all there are twelve or more pairs. The vitelline veins collect into a single large trunk (Fig. 5), *v.v.*, situated on the anterior side of the yolk-sac, and corresponding about to the sagittal plane of the embryo. The two trunks seen in the figure at the point of disappearance behind the head become confluent before actually entering the body.

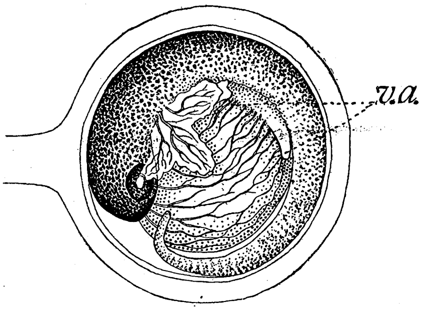

FIG. 6.

(2) *The Gills.* — These are of great size. They are three-lobed, the lobes being thin and delicate, much expanded, highly vascular, and widely confluent at their bases. The gills are so placed that their dorsal surfaces are close to, and concentric with, the inner surface of the egg capsule (Figs. 5 and 6). As they are functional during the intra-capsular life of the embryo

only, the term *allantoic gills*, first used by Gage ('90), I believe, is strictly applicable here. They begin at once to wither away when the embryo emerges from the capsule, the circulation being apparently cut off from them at that time. We placed one embryo in water immediately after its hatching and kept it there for some time, but could detect no trace of circulation in the gills, though it was always easily seen there during the intra-capsular life.

(3) *The Entire Absence of a Larval Period of Life.* — The young, at the time of hatching, possess none of the characters of aquatic amphibian larvæ. The external gills have, as already said, begun to wither and are not functional after the animal leaves the capsule. The gill-slits are imperforate, at least during the stages examined by us.

No suggestion of a dorsal and tail fin is present at any stage of development that has come under our observation. The tail is at all times as nearly round in section as is that of the adult. The just-hatched individuals, placed in water, appeared much distressed and were quite unable to swim. They sank immediately to the bottom and remained there until removed from the water.

The integumentary sense organs that are apparently invariably present in all aquatic urodele larvæ are, so far as we have been able to determine, entirely wanting here. We have carefully examined the skin both from the surface and on sections, and for various stages of growth, and always with negative results. Fig. 7 represents a specimen shortly after its escape from the capsule. The gills have almost entirely disappeared, and the abdominal walls are nearly closed over the yolk-sac. This specimen was 32 mm. long at hatching.

The color characters which distinguish the young during the first year have already been described. These are already assumed before escape, and are retained apparently until some time during the second year, when the almost black groundwork is changed to the dusky brown of the adult, and the fine silver specking is replaced by the much larger and less numerous yellow spots that mark the sides of the body of many of the adults.

In concluding this fragmentary contribution to the life history of this interesting salamander, we may remark that we are now directing our efforts to the securing of material, particularly embryonic material, that will enable us to complete the story. In the meantime we may call attention to some of the exceedingly interesting, but equally difficult problems of adaptation that are presented by our California salamanders.

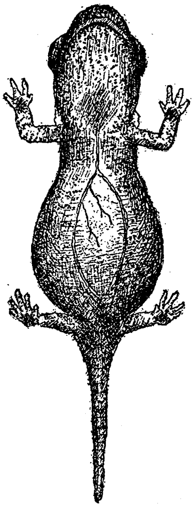

Fig. 7.

The species of Autodax appear to be among the most terrestrial of American Urodela.[1] They are, nevertheless, lungless, and are possessed throughout life of a delicate, smooth, moist skin. *Diemyctylus torosus*, on the other hand, which has practically the same geographical range, and hence is subject to the same climatic conditions, while being thoroughly aquatic for a considerable portion of its life, has developed an exceedingly hard and rough epiderm well fitted to resist desiccation ; and, besides, it possesses well-developed lungs. In other words, the adaptive modifications in the two forms have gone in directions opposite to what might have been expected. We should have supposed that whatever the immediate influences may have been which caused the disappearance of the lungs, these would have been most potent in animals that passed the most of their time in water; and we should likewise have supposed that it would be just the animals that lived exclusively on land, in the air, that would have taken on the dry, hard, rough epiderm. And the case is the more puzzling from the certainty which we have, Wilder (**'94**), that in some species at least, and hence inferentially in all, the lungless condition is secondary and not original. Were we permitted to suppose that the lungs had never existed in these species, we might then assume that the low grade of respiration required by the animals was taken on by the integument and buccal cavity when the gills disappeared, so easily that there was no particular demand for the production of lungs. But that *lungs already present should be lost by an air-breathing animal, and should be retained by a closely related water-living animal, is remarkable.*

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[1] Wilder's (**'99**) recent interesting paper on *Desmognathus fusca* and *Spelerpes bilineatus* shows that the former species approaches Autodax in this regard, but here there is a true aquatic larval period despite the fact that the eggs are laid on land. *Plethodon oregonensis* and *Batrachoseps attenuatus*, two geographical neighbors to Autodax, will be found, we are quite convinced, to be entirely terrestrial; but full evidence on the point is not yet at hand. And Wilder (**'94**) gives reason for supposing that *Plethodon erythronotus* is entirely terrestrial.

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